

GYNANDROMORPHISM IN THE WINTER STONEFLY GENUS *CAPNIA* (PLECOPTERA: CAPNIIDAE)¹

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ABSTRACT: A bilateral gynandromorph of *Capnia sequoia* is described from a single specimen collected in the San Joaquin Valley of California. This specimen represents the first recorded gynander in the plecopteran family Capniidae despite intensive collecting and observations made on thousands of specimens. Dorsal and ventral drawings are produced for the gynander along with those of normal specimens for comparison. The rarity of gynandromorphism in winter stoneflies is discussed. The term hypoproct is used for the male subgenital plate to distinguish it from the female subgenital plate.

While examining long series of many species of *Capnia* during our ongoing revision of the genus (Nelson and Baumann, 1987), we discovered a single specimen of *C. sequoia* Nelson and Baumann which exhibited bilateral gynandromorphism. Gynanders in stoneflies are rare with detection correlated with the sampling of great numbers of individuals. Only two accounts of plecopteran gynandromorphs are known from the North American literature (Ricker, 1965; Nebeker and Gaufin, 1966). Ricker (1965) described *Paraleuctra dusha* Ricker (Leuctridae) from a specimen he speculated could have been a gynander of *Paraleuctra occidentalis* since it seemed to be a mosaic of male and female parts. Later this species was reported as a nomen dubium by Zwick (1973). Stark et al. (1986) accepted this status in the most recent list of North American stoneflies. A ratio of one gynander per 500 specimens of *Zapada cinctipes* (Banks) and *Prostoia besametsa* (Ricker), both of the family Nemouridae, was given by Nebeker and Gaufin (1966) based on five gynanders per 2500 specimens. As part of our revision, over 18,000 specimens of more than 50 species of *Capnia* were critically examined and only one gynandromorph was found although various developmental aberrations were noted.

Additional reports of gynandromorphism have been made for specimens from other regions. Aubert (1958) noted gynanders in *Leuctra prima* Kempny and *L. fusca* (Linnaeus) from southern Europe. Two additional gynandromorphic specimens, one of *L. digitata* Kempny and one of *L. fusca* (Linnaeus) were examined by Klotzek (1971) along with a mention of another nemourid, *Nemurella pictetii* Klapalek in the possession of P. Zwick. A single record for gynandromorphism in the family Notonemouridae was reported by Illies (1961) for *Austronemoura chilena* Aubert from South

¹Received January 8, 1987. Accepted May 26, 1987.

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America. Based on these records, gynandromorphs have been reported in all the families of the Euhognatha except Scopuridae and Taeniopterygidae. Stanger (1982) makes no mention of gynanders or any malformations in her revision of *Taenionema* despite having examined large numbers of specimens. No cases of gynandromorphism are known from the Systellognatha nor from the Antartoperlaria (Zwick, 1973). This could be construed as evidence for the monophyly of the Euhognatha if a true tendency for gynandromorphic expression and viability exists. Long series of individuals of the systellognaths that come to light traps could be quickly scanned to possibly detect malformations in that lineage.

The gynander reported in this paper was collected from the mouth of Mill Creek in Fresno County, California on 17 February 1978 by L. Gilbert. Dr. Donald J. Burdick of Fresno State University made the specimen available to us for use during our revision. The species *C. sequoia* lives in smaller tributaries of the San Joaquin River system from the Tuolumne River south to the Tule River. This species is uncommon in collections resultant from both scant collecting in its range and small populations where it does occur. A total of 62 known specimens of this species exist in collections (Nelson and Baumann, 1987).

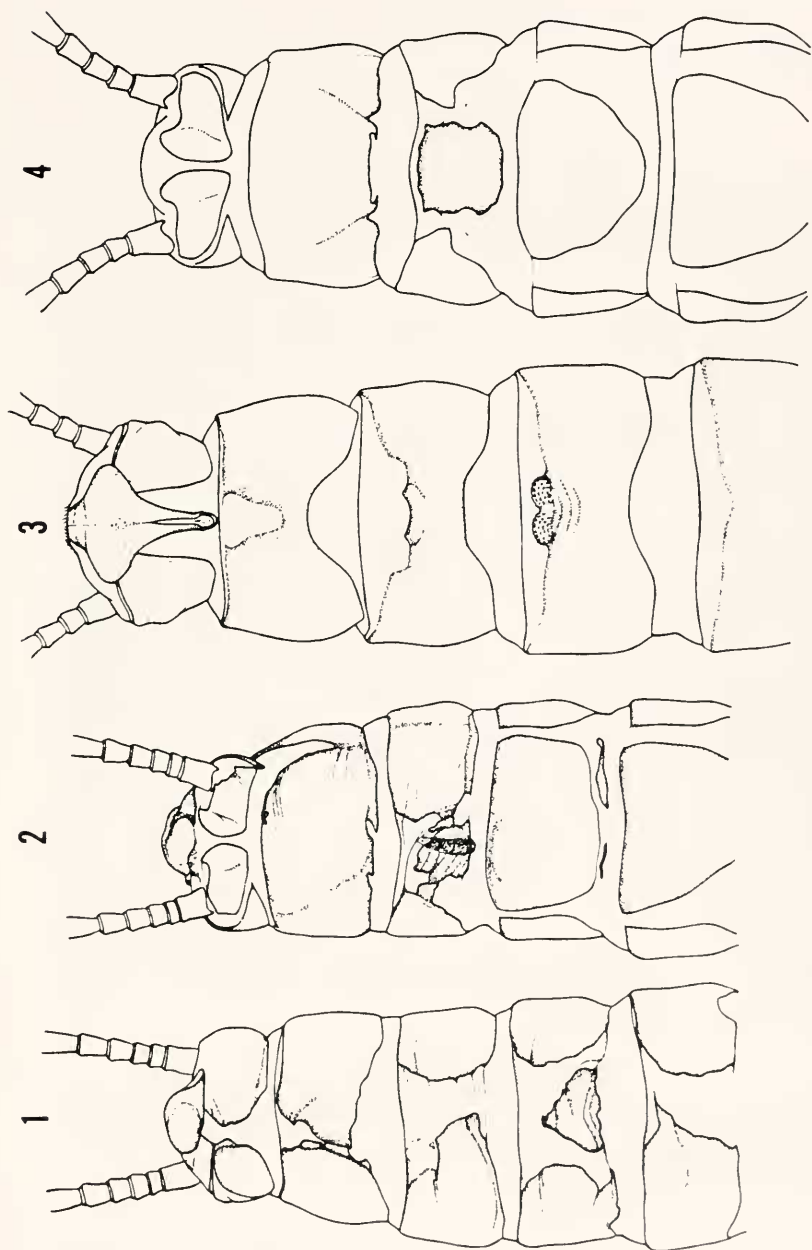
The specimen is bilaterally gynandromorphic on abdominal segments six through eleven with the right side bearing male features and the left side those of a female. In *Capnia* there is often a marked sexual dimorphism of the length of the wings but in this specimen the wings are of the same length on both halves of the body. No noticeable differences in symmetry exist anterior of abdominal segment one. In general habitus the specimen is of normal size and no structural aberrations that might have hindered movement are apparent. The specimen is somewhat teneral, with the male side more advanced in the tanning process than the female side. The male side is also more densely covered with setation.

Some key differences in the morphology of the male and female of *C. sequoia* occur in the extent of sclerotization of the abdominal segments. The characters used in the differentiation of species in *Capnia* are located on the dorsum of the abdomen of males and the venter of females. The mosaic of characters in the gynander present a unique opportunity to study the segment by segment homology in the genus and examine the often disparate, ambiguous (and confusing) terminology that has resulted from separate study of each of the sexes individually.

Dorsum. In normal females, abdominal terga two through eight are interrupted medially by a broad band of membrane while terga two through nine of the male are undivided, having a band of sclerotization covering the dorsum of each segment. Terga nine and ten of the female are undivided (without a

medial membranous area) while tergum ten of the male is distinctively divided forming a medial membranous area upon which the epiproct rests (Fig. 3). The gynander embodies a curious mosaic of the differences between the two sexes, with terga two through nine divided near the midline as in the female but with the male side ending abruptly near the midline (Fig. 1). The junction between the sclerotization on the female side and the medial membrane is very similar to that of a normal female while the junction between the male tergal sclerites and the membrane is malformed and resembles neither sex directly. One of the substantial differences between the tergal sclerotization of the male and female of *C. sequoia* is the lack of tergal knobs on the dorsum of the abdomen in the female. In the gynander these tergal knobs on segments seven and nine are expressed only on the male side (Fig. 1). The male epiproct on segment eleven is surprisingly well-developed on the right side, extending past the midline toward the female side resulting in the tip being basically normal in form although it is twisted to the left of the specimen (Fig. 1). However, just to the left of the tip of the epiproct the male features disappear and the female characters of a simple lobe-like segment eleven are expressed. A basal pad of sensilla is present on the base of the epiproct (ventral view) on the right side as in normal males (Fig. 3) and is absent on the left side (Fig. 1). The interface of the two sides relative to the epiproct is membranous and open and one is able to examine the internal structure of the epiproct by looking in from the female side.

Venter. The venter of the two sides of the gynander are basically similar from the head to segment seven of the abdomen. Sternum seven is somewhat darker on the left (female) hind margin due to internal sexual organs showing through the exoskeleton (Fig. 2). The subgenital plate of the female is evident on the left side of sternum eight including the heavily darkened sclerotization of the internal vaginal cavity (Figs. 2 and 4); no differentiation is noted on the male portion of sternum eight. Lateral notches are present on the anterior margin of sternum nine as in normal female specimens (Fig. 4). These notches are absent in males. The notch normally on the right side of the body is expressed near the midline in the gynander (Fig. 2). The hind margin of sternum nine is rounded and more heavily sclerotized on the right side as in male specimens and square and less sclerotized on the left side as in female specimens. The right posterior margin of sternum nine is notched, separating the sternum and tergum by a significant band of membrane, as in males. The left side of sternum nine is separated from tergum nine by a narrow suture, as in normal females. The paraprocts are both similar to those of a female although some malformation of the paraproct of the right side is observable with an incompletely formed medial margin, resembling half of



Figs. 1-2. *Capnia sequoia* gynandromorph; 1, dorsal; 2, ventral. Figs. 3-4. *Capnia sequoia*; 3, normal male, dorsal; 4, normal female, ventral.

the fusion plate (Hanson, 1946). The cerci are identical on both halves of the gynander. No sexual dimorphism with respect to cerci is apparent in normal specimens.

DISCUSSION

Agnew (1979) reported that most gynanders in Ephemeroptera are predominantly female with some male areas, with the male areas never comprising more than half of the individual. He further mentioned that the mosaic distribution of maleness and femaleness in gynanders of Ephemeroptera were compatible with an interpretation that gynanders arise from an XX female zygote with early loss of an X in one cell line. The tissue having lost the X chromosome would thus be XO, and would produce male structures. The specimen reported in this paper as well as those reported previously in Plecoptera differ with those seen by Agnew in that all tend to be more or less bilateral gynandromorphs. Despite this difference of bilateral or mosaic expression, the mechanism for the appearance of gynanders in Plecoptera could be the same as for Ephemeroptera. The difference probably results from less mixing of cleavage nuclei during the syncytial divisions in Plecoptera (as in *Drosophila*) than in Ephemeroptera.

A unique opportunity was offered by this bilateral gynandromorph for studying homology of sclerites between the two sexes. The segment numbering systems of the two halves of the gynander were consistent with accepted usage in the literature for each sex (Hanson, 1946; Brinck, 1956; Harper and Stewart, 1984), however, usage of the term subgenital plate for each of the sexes should be clarified. In females of *Capnia* and other Plecoptera the term subgenital plate is used to designate the medial portion of sternum eight. This usage is clear and valid since this plate overlies the gonopore. In males of *Capnia*, the term subgenital plate is used in conjunction with sternum nine which is basal to the paraprocts. This confusion of definitions of the term subgenital plate for the two sexes is unnecessarily ambiguous since more specific terms have been proposed in the literature for the subgenital plate of the male (e.g. hypoproct, Baumann, 1975; hypandrium, Crampton, 1918). The usage of the term hypoproct to designate this sclerite is preferred in combination with parallel terms of epiproct and paraproct to signify those sclerites surrounding the anus which are so useful in the taxonomy and classification of Plecoptera.

ACKNOWLEDGMENTS

We thank D.J. Burdick of Fresno State University for the specimen used for this study. We especially thank J.A. Stanger for the drawings and the Department of Zoology, Brigham Young University for financial support.

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